THE SENSITIVITY OF ECHOLOCATION IN BATS

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The full significance of acoustic orientation in bats can only be understood when we know what kinds of objects are detected and at what distances. Is it true, as is often assumed, that echolocation is limited to very close ranges of a foot or two? To what extent can bats discriminate between different objects? Are they merely aware that something is or is not directly ahead, or does echolocation inform them about the distance, size, numbers, direction and speed of motion of whatever is returning the echoes? Insectivorous bats seem to use echolocation in the pursuit and capture of flying insects; do they distinguish between various kinds of insects? Some continue to hunt insects in the rain; how can they tell the beetles from the raindrops? It would also be helpful to know how the acuity of echolocation varies among the several groups of bats which employ quite different intensities and patterns of sound for echolocation (Möhres, 1953; Griffin and Novick, 1955; Griffin, 1958).

These and related questions call for a better understanding of the sensitivity and effective range of echolocation, and this paper describes some new measurements of the distances at which bats first react to the presence of small wires. Although the smaller species of bats often fly very close to large objects such as the walls of a room before showing any sign of awareness that something is ahead, they do change the pattern of their orientation sounds at somewhat greater distances. For example, a *Myotis lucifugus* commonly increases its pulse repetition rate from perhaps 5 to 10 per second before take-off to 15 or 20 per second during ordinary flight and to 50 or more per second when landing or dodging small obstacles. This increase is closely correlated with success in avoiding objects such as wires. The rate rises every time a normal or blindfolded bat approaches the wires, but deafened bats show no such increase as they fly up to wires which they cannot detect (Galambos and Griffin, 1942). We have utilized this characteristic increase in pulse repetition rate to determine the distance at which bats first react to obstacles of various sizes by thus changing the pattern of their emitted sounds, and the results demonstrate a greater range and sensitivity of echolocation than had previously been recognized.

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METHODS

Bats were allowed to fly in the rectangular room shown in Figure 1. This room is 10 meters long, 3.7 meters wide, and 2.4 meters high; it was free from furniture or obstructions other than the wires, three observers, and a microphone and camera mounted on tripods. Seven meters from the end of the room, marked A, was a row of vertical wires 30 cm. apart, and 5.5 meters from the same end, in an indentation in one wall, was an Auricon model CM-72 16 mm. sound motion picture camera with a 9.5 mm. lens. In all cases the flying bats stood out against the white background formed by the opposite wall, which was marked only by conspicuously numbered vertical stripes placed at 60-cm. intervals to provide a frame of reference. In each flight used in the present measurements, the bat was released close to point A and flew approximately straight towards the opposite wall, B, passing the wires 7 meters away from its starting point. Usually it turned in the remaining 3 meters or else landed on the end wall.

The observer who released the bat at point A noted its approximate distance from the wall opposite the camera as it flew towards and past the wires. A second observer turned the camera to follow the bat during its flight, which in a typical case approximated the dashed line of Figure 1. The third observer kept the microphone pointed towards the flying bat. The motion pictures showed the flight path of the bat as it appeared from the position of the camera silhouetted against the opposite wall, but a parallax correction (based on the first observer's notes of the bat's distance from the white wall) was necessary except when the animal was directly opposite the camera. The camera was so placed that any errors introduced by parallax were minimized in the region where the pulse repetition rate was beginning to change.

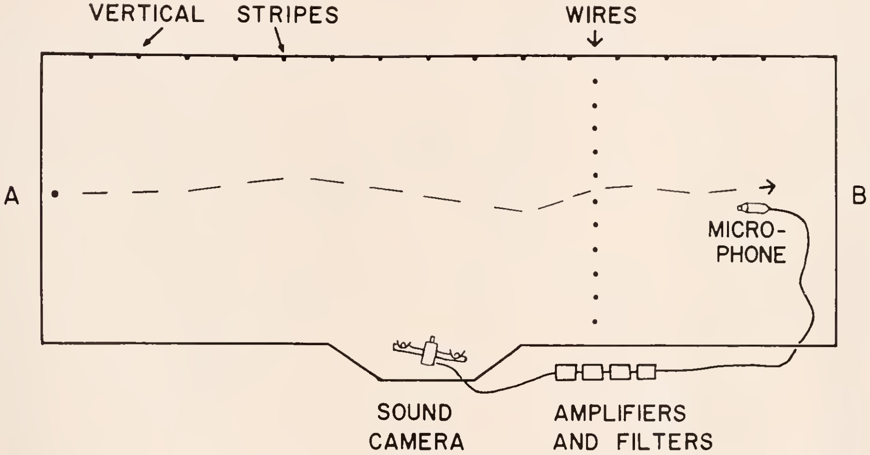

FIGURE 1. Diagram of room used for measurements of the distance of vocal reaction to the wires.

The high frequency sounds emitted by the bat as it flew the length of the room were picked up by a 640AA Western Electric condenser microphone placed 2.1 meters beyond the wires. The amplifiers and associated apparatus were similar to those used in previous studies of bat sounds (Griffin, 1950, 1953). The frequency band from 30 to 80 kc was selected by Spencer-Kennedy Laboratories model 301 and 302 variable electronic filters, 54 db/octave slope at 30 kc high pass and 18 db/octave slope at 80 kc low pass. The amplified signal was then passed through a detecting circuit (the pulse detector used by Griffin and Novick, 1955), and the resulting clicks were recorded directly on the sound track of the same film containing the photographs. The developed film was studied with a time-motion study projector, the single frames being projected one at a time while the corresponding portion of the sound track was moved past a celluloid time scale calibrated in milliseconds. It was thus possible to measure directly for every pulse the position of the bat and the elapsed time since the last pulse.

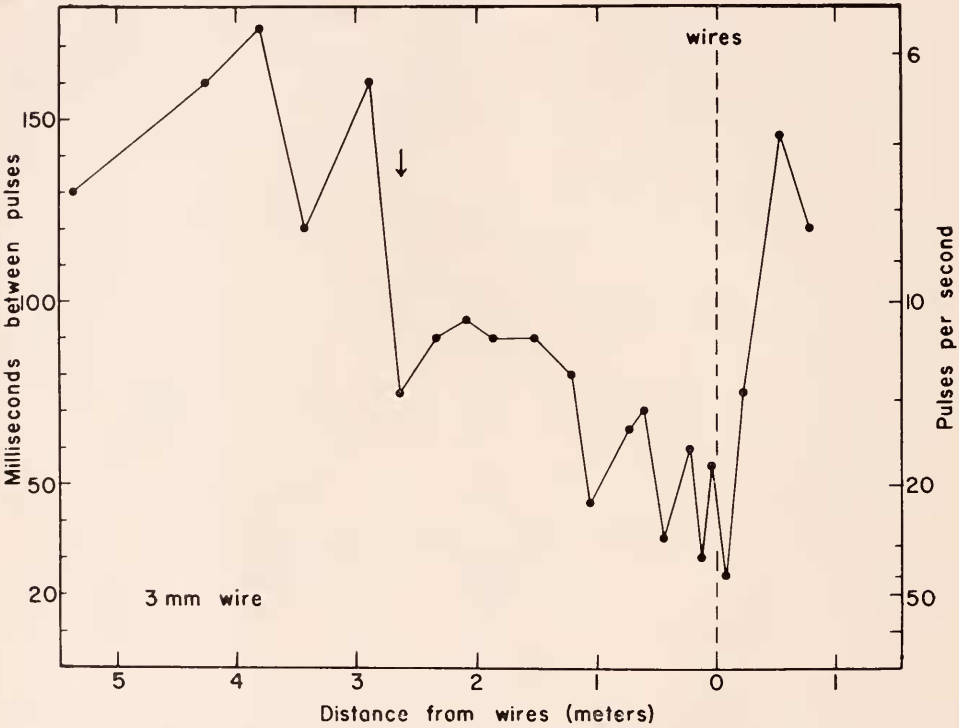

FIGURE 2. Variation of the pulse-to-pulse interval during one flight of a *Myotis lucifugus* through a row of 3-mm. wires along approximately the flight path shown in Figure 1. The arrow indicates the distance of the first vocal reaction.

The bats used in these experiments were *Myotis lucifugus* which had been in captivity for no more than one day, and all were in excellent condition. Six sizes of wire were used: 3 mm., 1.07 mm., 0.65 mm., 0.46 mm., 0.28 mm. and 0.18 mm. in diameter. The 3-mm. wire was rubber-covered, but all the others were bare iron or copper. Out of about 650 flights photographed, 146 were selected for analysis because the bats did react to the wires as demonstrated by straight flights through the wires, usually with a clear effort to dodge them. For this reason there was a larger proportion of misses than would otherwise have been the case. Flights with appreciable turns and flights near the walls, ceiling, or floor were excluded since a close approach to any object is likely to involve a change in pulse repetition rate. We also excluded flights in which the record of the pulses on the sound track was of low amplitude or was complicated by noise, so that there was a danger that some of the pulses might be overlooked in studying the record. Other flights were excluded because the pulse repetition rate varied widely during the 3 to 4 meters of straight flight from point A to the vicinity of the wires or did not return to approximately the same level after the bat passed through the wires. Nor were any flights used unless we were confident that the photographs established the bat's position with an accuracy of ± 10–15 cm. over at least the major part of its flight through the wires. The time required for sound to travel from bat to microphone was only about 0.03 second at the very most, and it decreased gradually as the animal flew towards the wires. Hence the acoustic delay had no appreciable effect on the measurement of the interval between pulses.

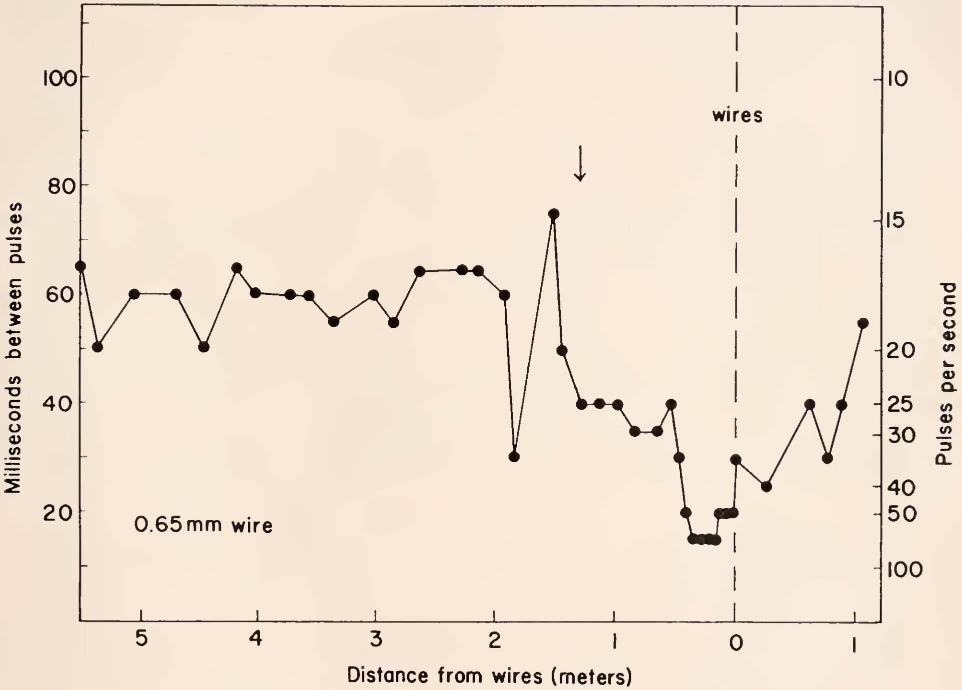

FIGURE 3. Intervals between pulses emitted by a bat flying through a row of 0.65-mm. wires.

RESULTS

More than 500 flights through the wires showed the characteristic increase in pulse repetition rate with only two or three exceptions, all of which occurred with the 0.18-mm. wire. For the 146 flights selected for analysis the bat's position was determined at the time each pulse was emitted, and the pattern of sound emission in typical flights is shown graphically in Figures 2–6, where each point represents a single pulse. Since the repetition rate varies rapidly it is more appropriate to consider the data in terms of the time interval between pulses. Therefore the ordinate of these graphs shows the time elapsed since the previous pulse, together with the corresponding repetition rate. Figures 2–6 show typical examples of these curves with five of the six sizes of wire studied, including cases when the pulse-to-pulse interval was both relatively constant (Fig. 6) or rather variable (Fig. 3) before the approach to the wires, cases in which the actual values of the interval were high (Fig. 2) or low (Fig. 3), and cases in which the drop was slight (Fig. 5) as well as others in which it was very marked (Fig. 4).

In the present experiments the wires were hung from small screw hooks in the ceiling, but the vocal reactions occurred when the bats were flying more than a meter below the ceiling, and thus were most unlikely to be reacting to the hooks. Furthermore, there were many similar hooks elsewhere on the ceiling which caused no change in the emitted sounds, and control tests with no wires hanging from the hooks showed no significant variations in the pulse-to-pulse interval. Each of fourteen bats for which clear records of the first flights are available yielded a typical curve like those shown in Figures 2–6 the first time it flew through the experimental room, showing that the change in pulse repetition pattern was not merely the result of familiarity with the position of the wires.

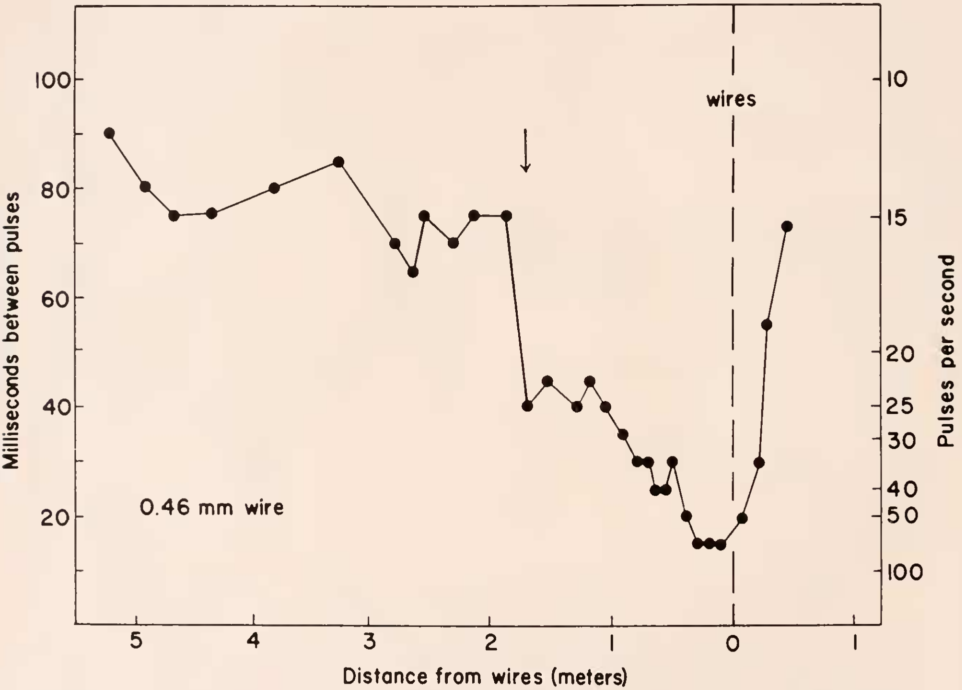

FIGURE 4. Intervals between pulses emitted by a bat flying through a row of 0.46-mm. wires.

The actual values of the pulse-to-pulse interval varied considerably. With a few individuals it was as high as 150–170 msec during the straight flight towards the wires (Fig. 2), with others it was approximately constant at 40 to 60 msec (Fig. 3). Just at the wires the interval sometimes fell to about 10 msec, but in

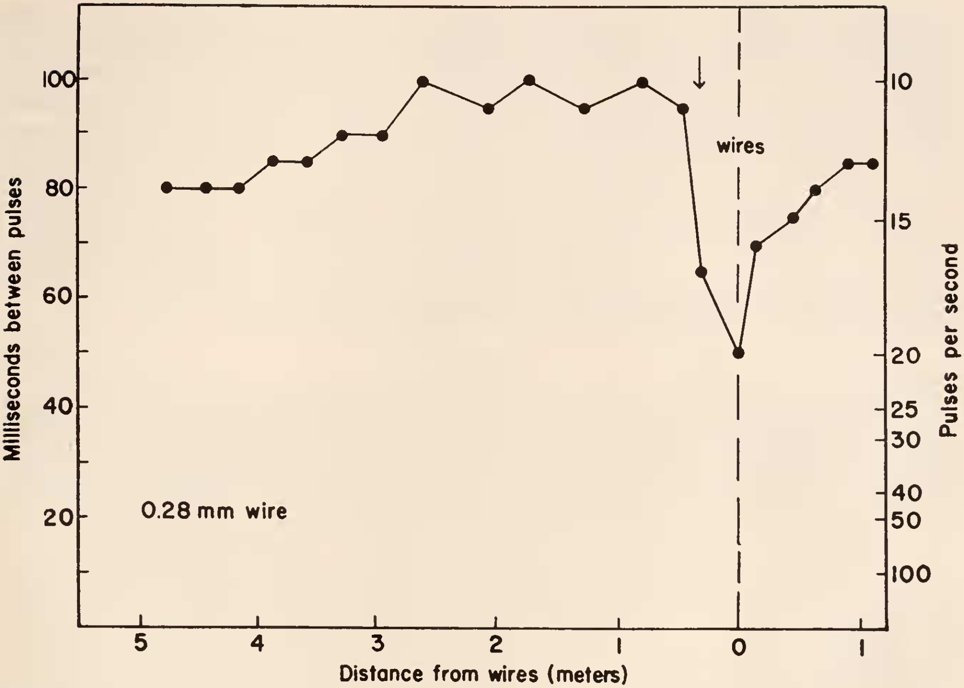

Figure 5. Intervals between pulses emitted by a bat flying through a row of 0.28-mm. wires.

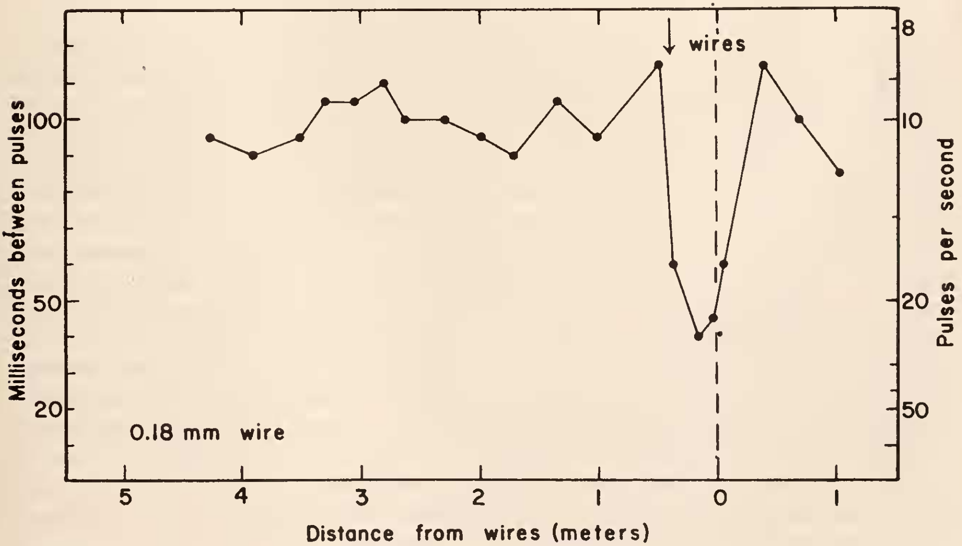

Figure 6. Intervals between pulses emitted by a bat flying through a row of 0.18-mm. wires.

other cases, especially with the smaller sizes, it fell only to 40 or 50 msec. Two methods are available for estimating the distance from the wires at which a first vocal reaction occurs with sufficient regularity to be significant. The first is to judge for each curve the approximate point at which the interval first fell significantly below the previous level and the level to which it returned after the wires had been passed. Such estimates could be made with some confidence within ± 15–20 cm., and examples are shown by small arrows on Figures 2–6. The average, minimum and maximum values of such estimates for each of the six sizes of wire are listed in Table I. It was encouraging to obtain nearly the same average distances of first reaction in completely independent series of photographs with the same wires taken several months apart and using different bats.

TABLE I

Distance from wires of various sizes at which Myotis lucifugus first reacted by decreasing the interval between pulses. The wires used were vertical and spaced 30 cm. apart. The individual estimates of the distance of detection were made from curves similar to Figures 2–6; and average, minimum, maximum values of such estimates are shown below. Owing to the uncertainty of such estimates their average is lower than the distance of first reaction to the wires obtained from Figure 7

Diameter of wire (mm.)	3.0	1.07	0.65	0.46	0.28	0.18
No. of bats	10	17	6	6	3	3
No. of flights	29	42	21	17	13	19
Per cent misses	93%	97%	76%	82%	77%	74%
Average est. distance of detection (cm.)	186	144	133	118	92	66
Range	(66–294)	(49–197)	(66–245)	(69–180)	(30–138)	(30–117)
Distance of detection obtained from Fig. 7 (cm.)	215	185	150	120	105	90

A second, and probably better, method is to average the values of the pulse-to-pulse interval measured at various distances from the wires. The results of this type of averaging are shown in Figure 7, together with arrows to indicate the distances at which these average curves first showed a definite drop below the level characteristic of flight before and after approach to the wires. As shown in Table I these estimates of the average distance of first reaction are somewhat greater than those obtained by the first method, presumably because variation due to other factors than proximity to the wires was cancelled out to some extent in the averaging process. Therefore the values obtained from Figure 7 provide the best available measure of the distance at which alert and successful bats of this species first react to wires of these six sizes. Consideration of Figure 7 is somewhat complicated, however, by the fact that not all of the individual curves covered the same range of distances from the wires. Hence the ends of the average curves are based on a smaller number of flights than is listed in Table I. Careful examination of the individual curves did not disclose any significant effects on the average curve of this change in number of flights, and in those more important portions of the average curves that are shown in Figure 7 by solid dots, 90% or more of the number of flights listed in Table I were included in the averages.

Table I shows that with all six sizes of wire there was a large proportion of misses, the remaining flights being "touches" or "hits" as defined by Griffin and Galambos (1941). Study of the few individual curves for touches or hits in the present series showed no appreciable difference from those ending in a miss. This is not inconsistent with the observation of Galambos and Griffin (1942) that there was less likely to be a change in rate in flights ending in a hit, because the present series was initially selected to include only straight flights by bats that were registering a high degree of success at dodging the wires.

Discussion

These measurements are an extension of earlier experiments in which the pulse repetition rate was shown to increase as bats approached wires that were about 1.2 millimeters in diameter. It is therefore important to point out certain differences in the methods used and in some aspects of the results obtained. The apparatus available for the earlier studies was not capable of reliably registering bat pulses at a sufficient distance to provide information such as that presented in Figures 2–7, even if the bat's distance from the wires had been recorded. Furthermore the room was smaller (4.5 meters long instead of 10 meters in the present experiments), and the flights studied were not limited to straight approaches by bats at their optimal level of skill at echolocation. This is probably why a higher proportion of the present series were misses, and why almost every one of the present trials showed a clear decrease in pulse-to-pulse interval as the bat approached the wires. More sensitive apparatus might well have revealed a larger proportion of cases with a slight but detectable change in repetition rate, had it been available in 1941. But this does not alter the fact, demonstrated at that time, that successful bats are much more likely to show a marked change in repetition rate on approaching small obstacles than are those which collide with the wires.

In the original experiments it was our impression from visual observation that the bats ordinarily reverted to a distinctly lower pulse repetition rate just *before* passing through the wires. It is therefore of interest to examine the more extensive and accurate data obtained in the present experiments with respect to the positions at which the pulse-to-pulse interval rose again to approximately the value measured before the bat approached within two meters of the wires. It is clear from the individual flights illustrated in Figures 2–6, as well as from the average curve for each size of wire, that the interval did not completely return to its earlier level until some distance past the wires. In several individual curves, however, the pulse-to-pulse interval appears to have risen shortly before the wires were passed, as in Figure 3. But many other individual curves, such as Figures 2 and 4, show that the pulse-to-pulse interval did not rise appreciably until the wires had been passed. It should be recalled in this connection that the position of the bat was determined only within ± 10–15 cm., and in a majority of individual curves the increase in interval occurred within this distance of the wires. In a substantial minority of cases the first definite increase appeared to be delayed until the bat was more than 15 cm. past the wires (8 out of 29 flights with 3-mm. wire, 17 out of 42 with 1.07-mm., 8 out of 21 with 0.65-mm., 4 out of 13 with 0.46-mm., but only one out of 13 with the 0.28-mm. and 3 out of 19 flights with the 0.18-mm. wire). In only one case, with the 0.28-mm. wire, the curve began to rise more than 15 cm. before the plane of the wires.

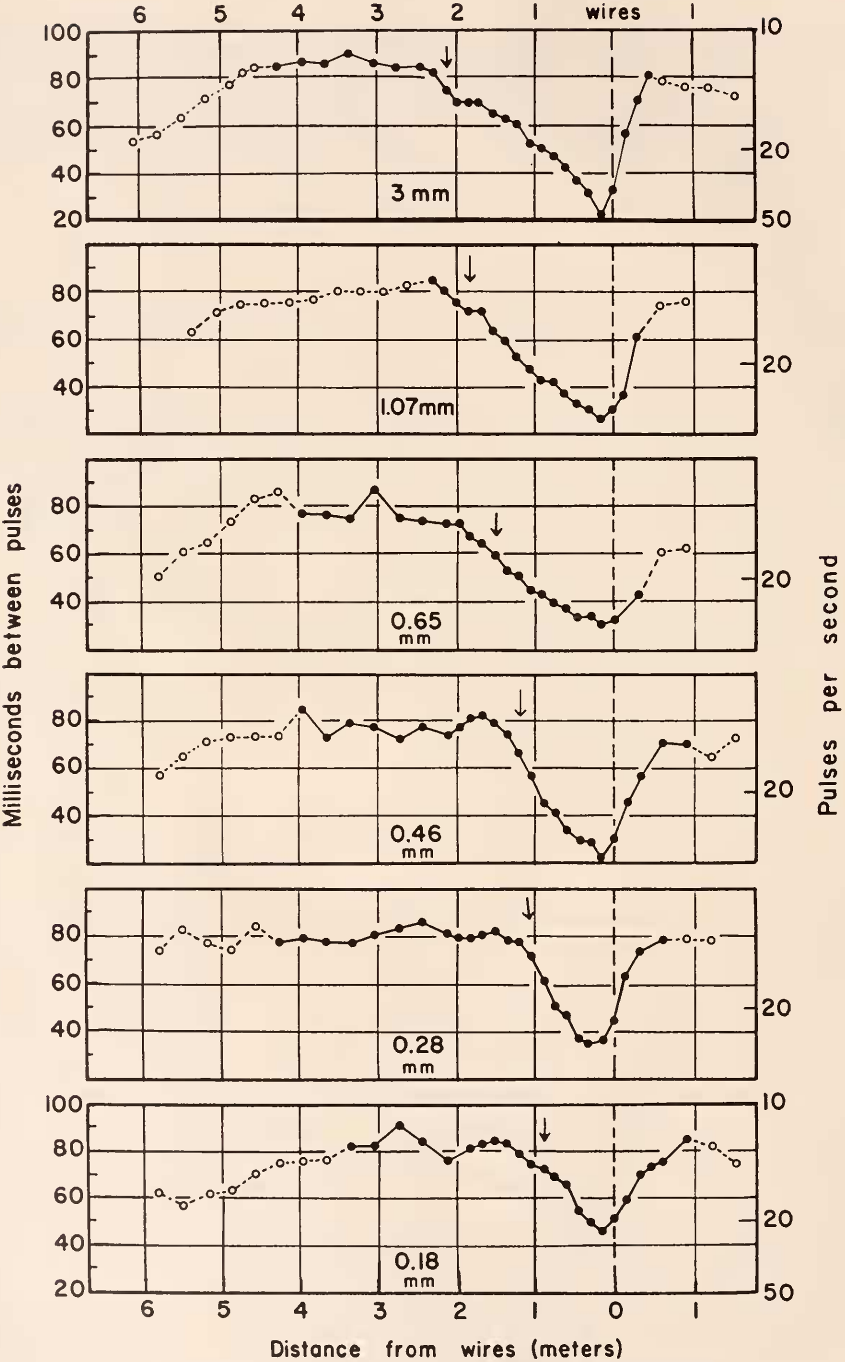

FIGURE 7. Average pulse-to-pulse intervals of bats flying past wires ranging from 0.18 to 3 mm. in diameter. The arrows indicate the distance of first vocal reaction.

The average curves of Figure 7 show a slight increase in the interval just as the bats flew past the wires. But since the possible error of the determinations of the bat's position was ± 10–15 cm. this small difference is only barely significant. In short, these measurements demonstrate only that the rise in the interval between pulses occurred on the average within 15 cm. of the wires, and was apparently more likely to begin shortly before passage through the plane of the wires than shortly after. Yet the 1.07-mm. wire was approximately the same size as the wires used in the earlier tests, and the spacing of the wires was the same. It is not clear whether the difference between our strong impression from observing the first experiments and the results of these more accurate measurements resulted from the selection of more alert and skillful bats for the present series, from the larger size of the room, or from some other factor.

In many flights the pulse-to-pulse interval just before the bat reached the wires alternated somewhat regularly between two quite different values, as in Figure 2. In other words the pulses tended to come in pairs, each pair separated from the next by an interval somewhat greater than that between the members of each pair. A similar tendency for pulses to occur in groups of two, three or occasionally four, was apparent in the first graphic records of bats' orientation pulses (Galambos and Griffin, 1942). Perhaps these groups correspond to the respiratory cycle. In the present series of curves the presence of this feature is clearly correlated with the size of the wires themselves, as shown in Table II.

TABLE II

Number of flights showing a marked alternation in the interval between pulses, similar to that illustrated in Figure 2

Diameter of wire (mm.)	Definite alternation		No alternation		Doubtful	
	Number	Per cent	Number	Per cent	Number	Per cent
3.0	25	86%	2	7%	2	7%
1.07	23	55%	11	26%	8	19%
0.65	12	57%	4	19%	5	24%
0.46	5	26%	10	53%	2	11%
0.28	1	8%	10	77%	2	15%
0.18	2	10.5%	15	79%	2	10.5%

Whatever significance this alternation may have, it was more likely to occur with the larger sizes of wire. Perhaps there was simply not time during the last quarter of a second or so of flight up to the 0.18- or 0.28-mm. wire for so complicated a vocal reaction. Indeed, if the decrease in pulse-to-pulse interval did not occur until the bat was closer than one meter to the wires, the period of increased repetition rate often contained only five or six pulses. Whatever additional information the bat obtained from the extra pulses over and above those that would have been produced at the previous rate, its vocal reaction was a brief and limited one.

The pattern of sound emission has been discussed above in terms of time, but it is also of interest to consider it in terms of space. The same photographs show how fast the bats were moving towards and past the wires, and the average of 54 velocity measurements was 3.9 meters per second, with the extremes of the series 2.4 and 6.3 meters/second. The speed did not vary significantly with the different sizes of wire, nor at different portions of the individual flights, except in a few cases when a late turn to dodge a wire caused momentary slowing and fluttering. Since the interval between pulses averaged about 70 milliseconds before the repetition rate had increased in proximity to the wires, a flight velocity of four meters per second means that one pulse was emitted about every 28 cm. As the bats flew within 0.5 meter of the wires the interval often fell to 20–30 msec, and the lower figure corresponds to one pulse every 8 cm. of flight at 4 meters/sec., or approximately once every time the bat moved through a distance equal to its own length. When the flight slowed in front of the wires, even shorter distances separated the positions at which successive pulses were emitted.

The actual detection of an echo from the wires must of course have preceded the first vocal reaction of the bat, and hence the distance of detection was somewhat greater than the distance of reaction discussed above. To consider the 3-mm. wire, for example, the average distance of reaction was 215 cm. But the first pulse to occur after a shortened interval was not registered until it had travelled to the microphone located 210 cm. beyond the wires, or 425 cm. from the bat. The acoustic delay for this distance is about 13 msec. A further correction should be made for the bat's reaction time, which might have been as little as 15 msec (the approximate time required for the contraction of the intra-aural muscles at the onset of a loud sound), or perhaps it was as long as 200 msec (the order of magnitude of minimum human reaction times). A conservative estimate of 25 msec for the sum of acoustic delay and reaction time indicates that when a bat detected the echoes of the 3-mm. wires it was at least 10 cm. farther from the wires than our data demonstrate directly. A similar estimate for the 0.18-mm. wires places the bat about 100 cm. when their echoes first became audible. If this does not appear to be a very impressive range of detection it is well to bear in mind that it is about 5500 times the diameter of the wires themselves.

The success of bats in avoiding wires naturally varies with the diameter of the wire; but even when wires are spaced 30 cm. apart the percentage of misses of an alert *Myotis lucifugus* does not fall sharply until the diameter of the wire is reduced below about 0.3 mm. In a long series of experiments with this species performed by Curtis (1952) in a smaller flight room, the average percentage of misses of wires spaced the same distance apart varied as follows with the wire diameter: 4.8 mm., 85%, 1.21 mm., 85%, 0.68 mm., 77%, 0.35 mm., 72%, 0.26 mm., 52%, 0.12 mm., 39%, and 0.07 mm., 36%. The chance score at this spacing is about 35%. These bats had been less highly selected for skillful flight and obstacle avoidance than those in the present series. For example, the three bats tested with 0.18-mm. wire registered 32 misses out of 46 flights photographed. The only selection involved in this series was the decision that the bat was flying well and tending to head straight towards the wires so that it was worthwhile to take pictures of it.

In view of the small size of the wires, relative to the wave-lengths of the emitted sounds, it is surprising that the distance of detection did not vary more with wire size. While the ratio of wire diameters was about 17:1, the distances of reaction varied only by less than 2.5:1. If Raleigh scattering was the chief source of the echoes, the ratio of echo intensities at a fixed distance should have been $(17)^4$:1

(Morse, 1948). To be sure, the echo intensity also varies inversely as the cube of the distance (since the echo radiates from wires as a series of cylindrical waves), and atmospheric attenuation reduces the echo somewhat further. Even if we assume the echo intensity to vary inversely as the fourth power of the distance, we still face a puzzling discrepancy of $(17)^4/(2.5)^4$ or more than two thousand.

One way to escape from this dilemma is to postulate that much higher frequencies or shorter wave-lengths are used to detect these small wires, perhaps harmonics of the fundamental frequencies in the bat's orientation pulse. This might bring the wire diameters up to the order of one wave-length so that Raleigh scattering would not predominate, and the echo intensity would vary more slowly with wire diameter. But all available evidence indicates that the maximum intensity of the emitted pulse, and the maximum sensitivity of hearing, both occur at about 50–60 kc, or a wave-length of 6 to 7 mm., where all but the two larger sizes should be within the range of Raleigh scattering. At higher frequencies the echo intensity and the sensitivity of hearing would probably both fall off fairly rapidly.

Another and perhaps better explanation would be that the bats could actually detect the wires at greater distances than our data indicate, but that they do not trouble themselves to increase the pulse repetition rate until they come within a meter or two. The relatively small increase in distance of vocal reaction between the 1.07- and 3-mm. wire could be explained about equally well by assuming that the echo strength increased less rapidly as the wire diameter approached one wave-length, or by postulating that the 3-mm. wire was detected at a greater distance but did not elicit a vocal reaction until about two meters. We cannot resolve this question without new and more refined experimental evidence. It is interesting to note in this connection a suggestion of a double break in the curves for the 1.07- and 3-mm. wires. It is possible that a slight reduction in the pulse-to-pulse interval occurs somewhat earlier than the onset of the pronounced drop which is apparent at all six wire sizes. About one-third of the individual curves for the 3-mm. wire have a distinct double break, as shown, for example, in Figure 2.

Since these insectivorous bats apparently detect small wires at 1.0 to 2.25 meters it is natural to inquire whether larger objects can be located at correspondingly greater distances. One factor which limits a simple extrapolation to larger sizes and longer ranges of detection is the attenuation of high frequency sound in air. (For values of the coefficient of atmospheric absorption in the bats' frequency range see Beranek, 1949, pages 64–72.) Furthermore the intensity of the echo falls off as approximately the third or fourth power of the distance, depending upon the geometry of the object reflecting or scattering the sound. Nevertheless it must be possible for these bats to detect objects several centimeters in size at considerably greater distances, and really large objects such as trees or buildings are presumably detectable at distances of many meters. No methods have yet been devised, however, to determine objectively the maximum distances at which such objects are first detected by bats, and this fact presents a real challenge to future students of echolocation and bat behavior.

SUMMARY

1. The distance at which bats (*Myotis lucifugus*) react to the presence of a row of small wires has been measured by a photographic determination of the

distance at which the pulse repetition rate first increases as the bats fly towards the wires. Distinct changes in this rate were measured in almost every flight towards wires spaced 30 cm. apart and ranging in diameter from 0.18 to 3 mm.

2. The interval between successive pulses averaged 60 to 80 msec as the bats flew along the room towards the row of wires, and dropped to 20–40 msec just before the barrier. The intervals decreased less with the smaller sizes of wire.

3. All but the largest of these wires are well below one wave-length of the emitted sounds of these bats (50–60 kc, or 6–7 mm., at the peak intensity and 120 kc, or about 3 mm., at the very beginning of some pulses).

4. Clear evidence that the wires had been detected was furnished at the point where the interval between pulses first dropped significantly below the level that prevailed before and after the approach to the row of wires. This average distance of first vocal reaction to the row of wires was 215 cm. for 3-mm. wire, 185 cm. for 1.07-mm., 150 cm. for 0.65-mm., 120 for 0.54-mm., 105 cm. for 0.28-mm., and 90 cm. for 0.18-mm. A conservative correction for reaction time and the acoustic delay between the bat and the microphone indicates that the distance of first detection must have been at least 10 cm. greater than these distances of reaction.

5. Since small wires can be detected at distances of as much as 5500 times the wire diameter, and well before the bat gives evidence by its flight pattern that it is aware of them, it appears likely that larger objects are detected at considerably greater distances.

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